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A new species in the asterinid genus *Patiriella* (Echinodermata, Asteroidea) from Dhofar, southern Oman: a temperate taxon in a tropical locality

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CONTENTS

SYNOPSIS. The status of the hitherto temperate-water asterinid genus *Patiriella* is briefly discussed, including in its diagnosis details of actinal plate and ventral/lateral plate arrangement. A new species, *P. paradoxa*, is described from shallow water on the Dhofar coast of Oman. The distribution of *Patiriella* on the Dhofar coast is discussed in relation to the peculiar oceanographic conditions and vicariant events in the region.

INTRODUCTION

Although one of us (ACC) made extensive collections along the coasts of the Sultanate of Oman between 1983 and 1990 (Campbell and Morrison, 1988 and Marsh and Campbell, 1991), the echinoderm fauna of southern Arabia remains incompletely known. However, those echinoderms which have been recorded are tropical species or endemic species with tropical affinities (Clark and Rowe, 1971; Price, 1982; Campbell and Morrison, 1988; Marsh and Campbell, 1991). The discovery (by FWER) of three specimens of a new species of the predominently temperate-water, asterinid starfish genus *Patiriella* Verril (1913) among the Omani shallow water (less than 10m) collections from two sites in Dhofar therefore poses a paradox.

Here we briefly discuss the status of the genus *Patiriella* and describe fully the new species. This work attempts to explain the presence of an otherwise temperate-water echinoderm genus in this tropical location, given the peculiar local oceanic conditions which include upwelling (see summary by Campbell and Morrison, 1988), and past vicariant events.

The type specimens have been deposited in the Natural History Museum, London U.K.

SYSTEMATIC DESCRIPTION

PATIRIELLA Verrill

Patiriella Verrill, 1913: 483; 1914: 263; Fisher, 1919: 410; H.L. Clark, 1946: 134; Dartnall, 1971: 39; A.M. Clark and Courtman-Stock, 1976: 80; A.M. Clark, 1983: 365; A.M. Clark and Downey, 1992: 192.

TYPE SPECIES. *Asterina (Asteriscus) regularis* Verrill, 1870 (1867); by original designation.

DIAGNOSIS

After A.M. Clark in A.M. Clark and Downey (1992), amended.

A genus of Asterinidae with five to about eleven short rays (R up to c. 60mm); pentagonal to stellate in outline; aborally arched; primary abactinal plates in two 'fields', a slightly irregular radial (usually the midradial and first dorsal-lateral series on either side) 'field' and a regular lateral 'field' on either side; mid-radial abactinal plates with proximal edge trilobed or simply crescentic; the proximal concave sides of abactinal plates subtend spaces with usually one to several papular pores, separated by one to several small secondary plates; abactinal armament comprising relatively few (< 40 per plate) very coarse, almost granuliform, multipillared

spinelets; actinal plates distinctly aligned in oblique series between the second or third, and subsequent adambulacral plates and the inferomarginal plates and delimiting a membranous, proximal, triangular area which is usually filled by several plates; ventral-lateral angle of rays supported internally by abactinal plates which meet the actinal plates by virtue of the oblique alignment of both; towards the ray base as the ventral-lateral angle becomes less acute with ray depth, totally internalised plates, spanning between the abactinal and actinal plates, can be found; actinal armament coarse, short spines, mostly single, not more than two per plate; furrow spines usually two (sometimes one) per plate; subambulacral spines one (rarely two); suboral spines one to four or none; no pedicellariae.

Species included: *Patiriella brevispina* H.L. Clark, 1938; *Asterias calcar* Lamarck, 1816; *Asteriscus calcarata* Perrier, 1869; *Asteriscus chilensis* Lutken, 1859; *Asterina dyscrita* H.L. Clark, 1923; *Asterias exigua* Lamarck, 1816; *Asterina fimbriata* Perrier, 1875; *Asterina gunni* Gray, 1840; *Patiriella inornata* Livingstone, 1933; *Asterina oliveri* Benham, 1911; *Patiriella parvivipara* Keough and Dartnall, 1978; *Patiriella pseudoexigua* Dartnall, 1971 (with subspecies *pacifica* (Hayashi, 1977, as *Asterina*); *Asterina (Asteriscus) regularis* Verrill, 1870 (1867); *Patiriella vivipara* Dartnall, 1969b; *Patiriella paradoxa* sp. nov.

Other species *Patiriella nigra* H.L. Clark, 1938 and *Patiriella obscura* Dartnall, 1971 are considered to be conspecific with *P. oliveri* (Benham) and *P. pseudoexigua* Dartnall respectively by Rowe (*in* Rowe and Gates, 1995); *Patiriella tangribensis* Domantay and Acosta, 1970, is inadequately described and cannot confidently be assigned to this genus.

Remarks

The genus *Patiriella* Verrill, 1913, has had a rather chequered history. It has been considered a valid taxon by most recent authors (e.g. Fisher, 1919; H.L. Clark, 1928; 1938; 1946; Livingstone, 1933; Madsen, 1956; Dartnall, 1971; A.M. Clark and Rowe, 1971; A.M. Clark and Courtman-Stock, 1976; A.M. Clark, 1983; A.M. Clark and Downey, 1992) or a synonym of *Asterina* Nardo, 1834 (e.g. H.L. Clark, 1916; 1923; Hayashi, 1940; 1977; Mortensen, 1933 (as a subgenus of *Asterina*)). The history and current status of *Patiriella* has been most recently discussed by A.M. Clark (1983; 1992 (in Clark and Downey)) who commented (1992:178) that 'The very coarse and abbreviated, almost granuliform, armament of the upper side may warrant a supra-specific distinction from *A. gibbosa* of *P.*

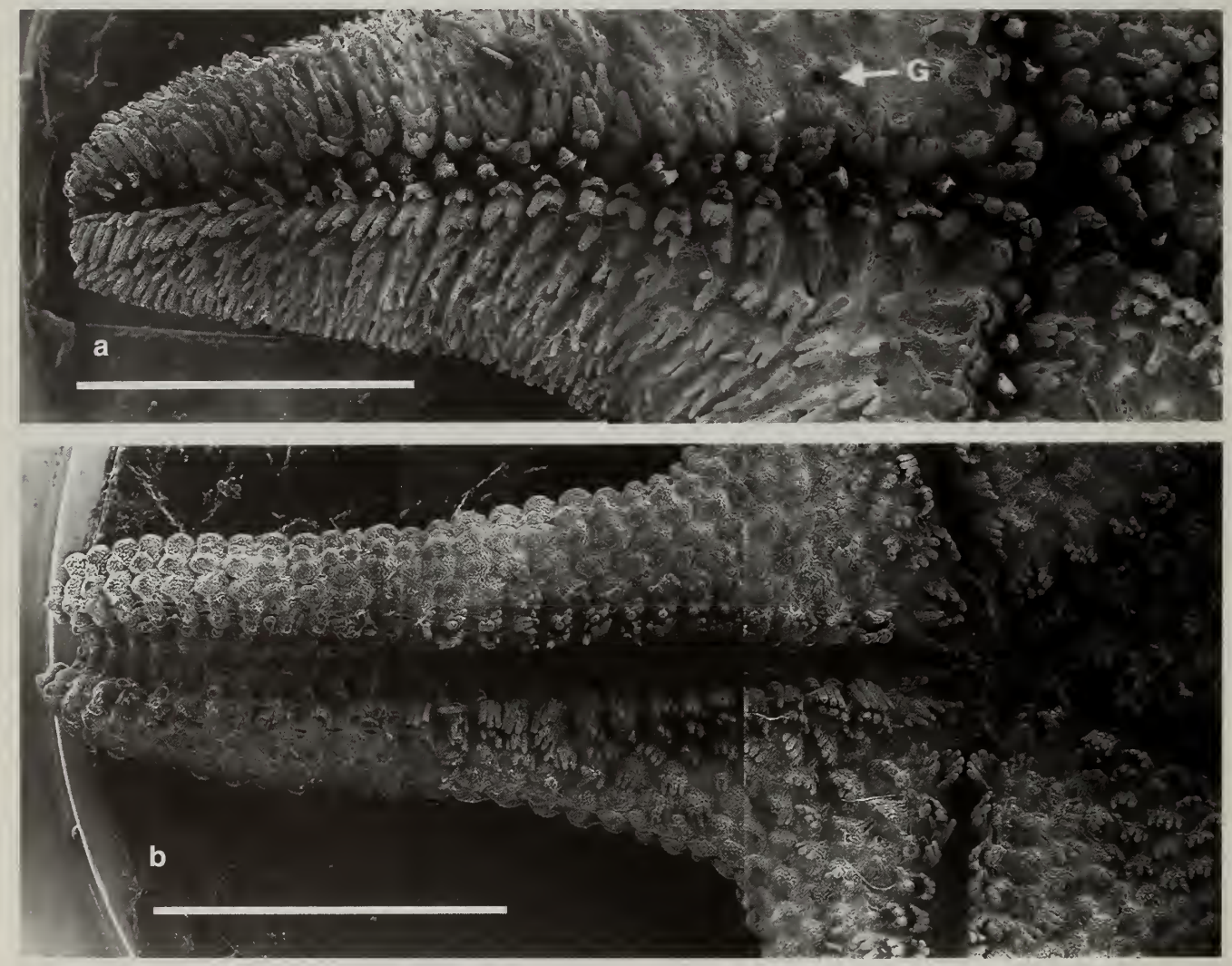

Fig. 1 a, Scanning electron micrograph of the actinial surface of *Asterina gibbosa* from Plymouth U.K. Scale bar = 5mm . G = gonopore; b, Scanning electron micrograph of the actinial surface of '*Asterina*' *cepheus* from Wadi Haart, Sadh. Dhofar, Southern Oman. Scale bar = 5mm

regularis together with *P. gunni* (Gray) and *P. calcar* (Lamarck) from Australia, also *P. exigua* (Lamarck) which extends from the Indo-West Pacific into the S.E. Atlantic'. She thought reassessment of the rank of *Patiriella* was best left to 'one of several Australasian specialists to determine . . .', retaining the species *exigua* as a member of the genus *Patiriella*. A new review of the family Asterinidae, including a reappraisal of the status of *Patiriella* is being undertaken by F.W.E.R. elsewhere. However, whilst in the present paper we acknowledge that a very close relationship exists between the genera *Asterina*, *Patiriella* and *Patiria* (Gray, 1840) (*Patiria* is considered a synonym of *Asterina* by Hayashi (1940) and A.M. Clark (1983 (in Clark and Downey, 1992)); we accept their separate generic status, until the matter is more clearly resolved, such a resolution being outside the scope of this paper [1]. In taking this stance, we have amended A.M. Clark's in Clark and Downey, 1992) diagnosis of *Patiriella* to include a description of the alignment of actinal plates (included by Verrill (1913) in his diagnosis of the genus) and the internal alignment of actinal/abactinal plates at the ventral/lateral angle (described by Verrill (1913) as a feature of the family Asterinidae). As a taxonomic character, actinal plate alignment has been largely ignored. The exception was Fisher (1917; 1919) who thought this a useful character when distinguishing his new genus *Paranepanthia* (type-species *Nepanthia platydisca* Fisher, 1913) in which the plates are aligned obliquely across the actinal surface, from *Asterina* in which he saw the actinal plates forming chevrons across each interradial area, the plates being aligned only parallel to the furrows along each ray. Fisher (1919) was, however, comparing *Paranepanthia platydisca* with the species '*Asterina*' *cepheus* (Müller & Troschel), and '*A*'. *coronata* (von Martens) and not the type species *A.gibbosa*. In accepting *Asterina* in this sense, Fisher was clearly not familiar with the fact that in the type-species, *A. gibbosa*, the actinal plates, as in *Patiriella* and *Paranepanthia*, are clearly aligned obliquely between furrow and margin Fig 1a & b (there is no question, however, that *Paranepanthia* is a valid genus (F.W.E.R.). A.M. Clark (1971, in A.M. Clark and Rowe) noted Fisher's work when identifying two specimens of an undetermined species of what she considered a *Paranepanthia* from Zanzibar. She considered (1971:71) the importance of actinal plate arrangement, as a functional and taxonomic character, required investigation. However, A.M. Clark (1983) did not expand further on this matter in her more recent revision of the family Asterinidae. Although a recent survey of the family by one of us (F.W.E.R.) does show actinal plate arrangement to be a useful character in distinguishing some of the genera, actinal plate arrangement undoubtedly has a functional role which is probably micro-habitat related. We include description of the internal structure of the ventral/lateral angle in our diagnosis following A.M. Clark (1983) who concluded that differences in arrangement of these internal plates were important in indicating taxonomic affinities, a conclusion supported herein, though on the basis also, that it may relate to ray shape within the family.

Patiriella paradoxa sp. nov.

DIAGNOSIS. Stellate species of *Patiriella* with five rays; abactinal plates of aboral, radial 'field' tri-quadrilobed, forming a delicate reticulum; papular areas each with three to six papulae and one to two secondary plates; no suboral spines; proximal actinal plates each with a single spine.

[1] Species attributed to *Asterina* s.s. from outside the Atlantic region are **NOT** congeneric with the type-species, *A. gibbosa* (Pennant), and require reallocation to other existing or new asterinid genera according to Rowe (in Rowe and Gates, 1995); the suggested recognition of *Asterinides* Verrill (1913) (type-species *A. folium* (Lütken)) as a valid subgenus of *Asterina*, by A.M. Clark (1983; 1992 (in Clark and Downey)) is supported, but at generic level, by Rowe (in Rowe and Gates, 1995).

HOLOTYPE. BMNH (dry) BMNH 1997.1016

TYPE LOCALITY. 0.5 km southeast of Wadi Haart and about 4km north east of Sadh village, Sultanate of Oman (17° 04'N, 55° 06'E), intertidal, just below level of the conspicuous barnacle *Tetraclita squamosa rufotincta*, collected together with *'Asterina' cepheus* (Müller & Troschel, 1842), A.C. Campbell 4 May 1987 (210050201) (fig.2).

MATERIAL. In addition to the holotype, two paratypes (dry). Paratype 1 BMNH 1997.1017, collected at the same locality with the holotype. Paratype 2 BMNH 1997.1018, Raaha, 2.5km west of Wadi Ayn, Sultanate of Oman (16° 58'N, 54° 50'E), c. 8m depth, on rocks amongst corals, coll. A.C. Campbell, 5 Dec., 1986 (210050202) (fig.2).

ETYMOLOGY. The species name (Lat. paradoxum) refers to the unexpected occurrence of this predominently temperate-water genus along an otherwise tropical coastline.

DESCRIPTION OF HOLOTYPE. (Figs 3 a & b; 4 a & b). Specimen stellate in outline, R=17.8mm, r=9.0mm, R/r=1.98; br=10.3mm (across base of ray between first superomarginal on each side), R/br=1.73. Orally flat, aborally arched. Rays more or less elongate triangular, tapering from a relatively wide base to a rounded tip. Centre of disc delimited by a complete ring of prominent, spinelet-bearing plates, outside of which a second, more or less complete ring of less prominent plates evident. The prominent, ovate madreporite occurs in interradius CD.

Beyond the central disc, the imbricating primary abactinal plates form two 'fields' along the rays. Radial 'field' comprising an irregular, zig-zag series of mid-radial (carinal) plates and the first dorsal-lateral row on each side. Shape of this 'field' elongate-leaf-shaped along the ray, tapering proximally and distally and widest at about ½R. Denuded plates deeply notched, mostly quadrilobed (X-shaped), but, at least between ½–¾R, some mid-radial plates tri-lobed (Y-shaped), the plates together forming a relatively delicate reticulum. Papular areas, between the plates, are relatively large, up to 0.8mm diameter, each subtending 3–6 papulae between which 1 or 2 minute, spinelet-bearing secondary plates usually occur. Primary plates with crystal bodies, except on their proximal, crescentic ridge which carries 5–7 granuliform spinelets in a single series; spinelets range from c. 0.30mm long × 0.12mm wide (straight sided) to about 0.37mm long × 0.14mm wide (these larger spinelets becoming club-shaped (0.18mm wide) towards their tip). Lateral 'field' comprising about 10 regularly arranged rows of plates at the base of the rays, closely imbricate with a deep proximal notch subtending 1–3 papulae occurring in the proximal half of the first 5 rows of plates, the papulae not extending to the superomarginal line. Lateral 'field' plates with crystal bodies and from 2–7 spinelets.

Ventral-lateral margin sharply delimited, however neither inferomarginals nor superomarginals significantly larger than immediately adjacent actinal or abactinal plates respectively. Inferomarginal plates aligned in the same plane as the actinal surface, slightly protrude laterally and bear a group of 2–3 minute spinelets. Superomarginal plates aligned vertically, correspond with the inferomarginals below them and bear 1–2 spinelets.

About 10 rows of actinal plates counted; the first two extending to the tip of the ray; plates are aligned both parallel to the furrow but also distinctly obliquely across the actinal surface between the adambulacral plates and inferomarginal plates. Oblique alignment accentuated both by the actinal spination and narrow, shallow

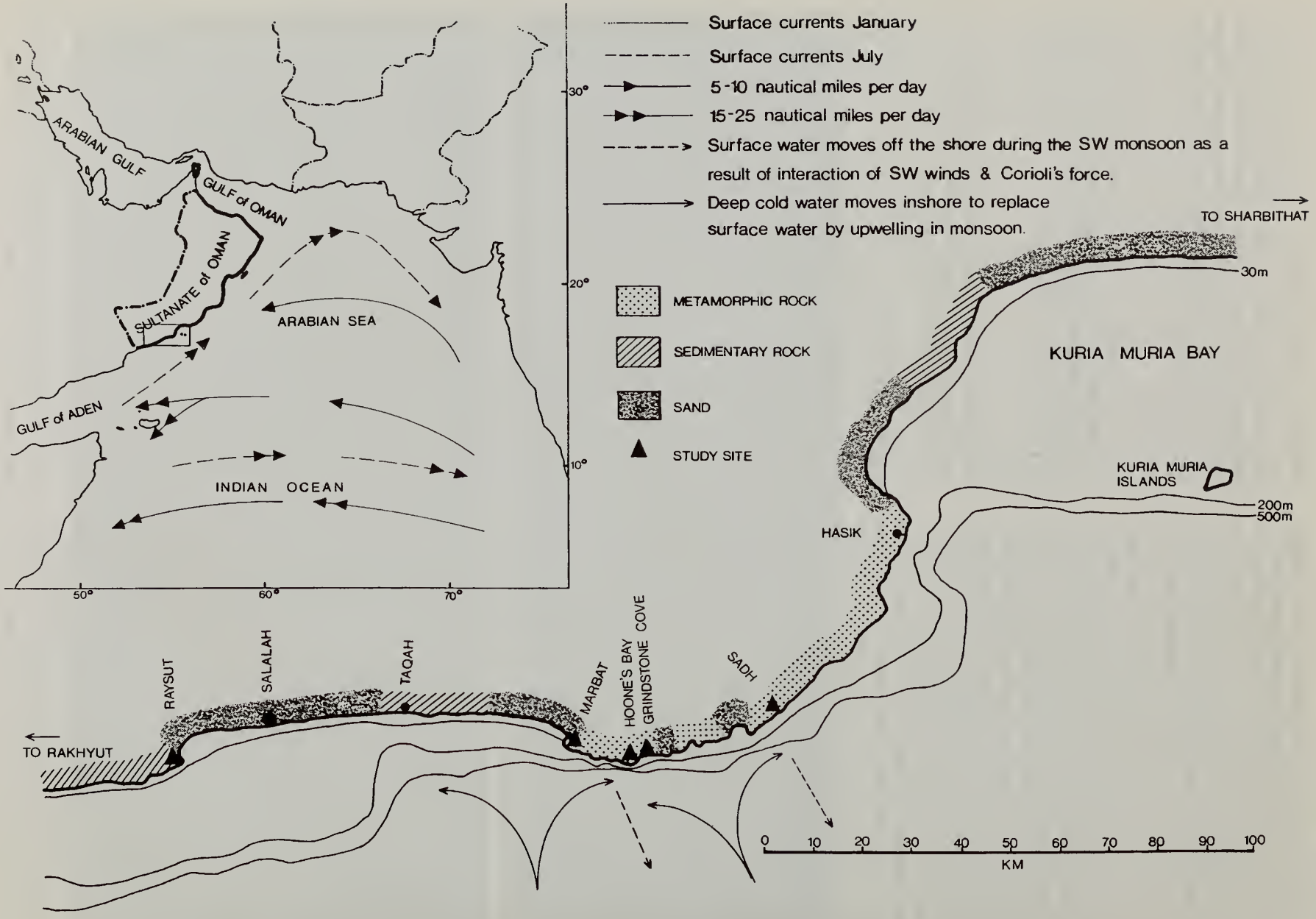

Fig. 2 Map of Dhofar, Southern Oman, showing submarine contours and monsoon events. Reproduced by kind permission from *Echinoderm Biology* (eds. R.D. Burke *et al*) 1988, published by A.A. Balkema, Rotterdam and Brookfield.

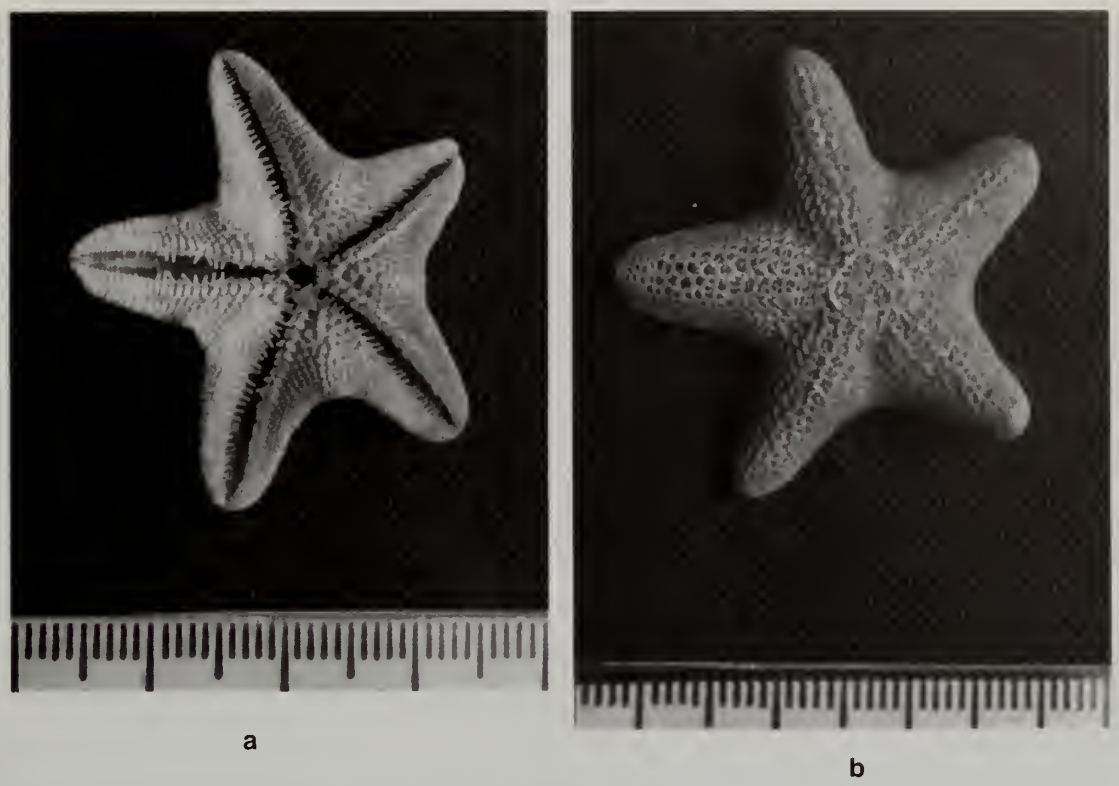

Fig. 3 a, Photograph of *Patiriella paradoxa*, Holotype, from Wadi Haart, Sadh, Dhofar, Southern Oman. Abactinial view. Scale in mm; b, Photograph of *Patiriella paradoxa*, Holotype, from Wadi Haart, Sadh, Dhofar, Southern Oman. Actinial view. Scale in mm.

furrows occurring between the oblique lines of plates. First complete oblique line of plates arises opposite the second adambulacral plate in each furrow, creating a triangular area bounded by the first adambulacral plates, distal edge of the oral plates and first oblique series in each actinal intermediate area. This proximal area occupied by 2 (interradii BC, DE and EA), 3 (interradius AB) or 4 (interradius CD) plates. A small circular patch of non-calcified skin (up to 0.6mm diameter) occurring adjacent to the distal edge of the oral plates in interradii AB, CD and EA. Actinal plates each bear a single, tapering spinelet (up to 0.64mm long × 0.30mm at base) on the proximal 80% of the actinal surface, the remaining distal plates with 2 small spinelets.

There are 28–29 pairs of adambulacral plates to each furrow. These are twice as wide as long. First 12–14 plates bear 2 tapering furrow spines, proximalmost more slender and shorter than distalmost spine (on adambulacral 3: distalmost spine measures 1.0mm long × 0.35mm wide, at base tapering 0.20mm wide near tip; proximalmost spine measures 0.78mm long × 0.23mm wide at base, tapering to 0.14mm wide near tip). Proximalmost spine becomes rapidly smaller and peg-like towards the 12th–14th plate, beyond which the adambulacral plates each bear a single furrow spine. A single, stouter, subambulacral spine (on adambulacral 3: 0.87mm long × 0.29mm wide, more or less cylindrical) occurs on each adambulacral plate. The oral plates each with 4 oral (furrow) spines of which the apicalmost is longest. No suboral spines.

Gonopores not occurring on the oral surface and cannot be distinguished aborally.

COLOUR. Dried holotype is a uniform, pale 'museum' buff colour. Colour in life is not recorded.

PARATYPE 1. BMNH 1997.1017 has R=19.0mm, r=7.9mm. R/r=2.4; br=9.4mm, R/br=c.2. Generally very similar in appearance to the holotype, differing only in minor detail. Two furrow spines occurring only on the 1st–4th adambulacral plates, thereafter the plates with a single furrow spine. Small patch of non-calcified skin occurs adjacent to the distal edge of the oral plates in each interradius, this proximal actinal triangle being filled by 1 (interradii CD, DE) or 2 (interradii EA, AB, BC) plates.

PARATYPE 2. BMNH 1997.1018 has R=19.0mm, r=10.00mm, R/r=1.9; br=11.2 mm, R/br=1.7. The dry specimen is contorted. It differs from the holotype and paratype 1 in the following features. Rays are slightly broader at their bases relative to their lengths. Aborally, centre of disc not delimited by a prominent ring or rings of plates. Radial 'field' of abactinal plates is compact, plates closely imbricating with only the ridge evident and bearing 5–7 spinelets. Papular areas contain 1–4 papulae and occasionally a single secondary plate. Actinal spinulation coarser, otherwise the plate arrangement closely similar to the other type specimens. Actinal proximal triangle filled by 1 or 2 plates, no patches of non-calcified skin evident. Some 36 pairs of adambulacral plates along each furrow; each bearing a single furrow and single subambulacral spine, with the exception of the first plate with a second, smaller proximal furrow spine. Furrow and subambulacral spines flattened along their length with a squared-off tip. Several furrow spines spaced along length of the furrow, with bifid tip. Oral plates and spines are similar to those of both the holotype and paratype 1. The paratype 2 is uniformly light grey in colour.

HABITAT. The holotype and paratype 1 were collected on 4.5.87, 0.5km. south east of Wadi Haart and about 4 km. north east of Sadh village. These were collected, together with *'Asterina' cepheus* intertidally on a gently shelving exposed rocky shore with tide pools just below the level of the conspicous barnacle *Tetraclita squamosa*

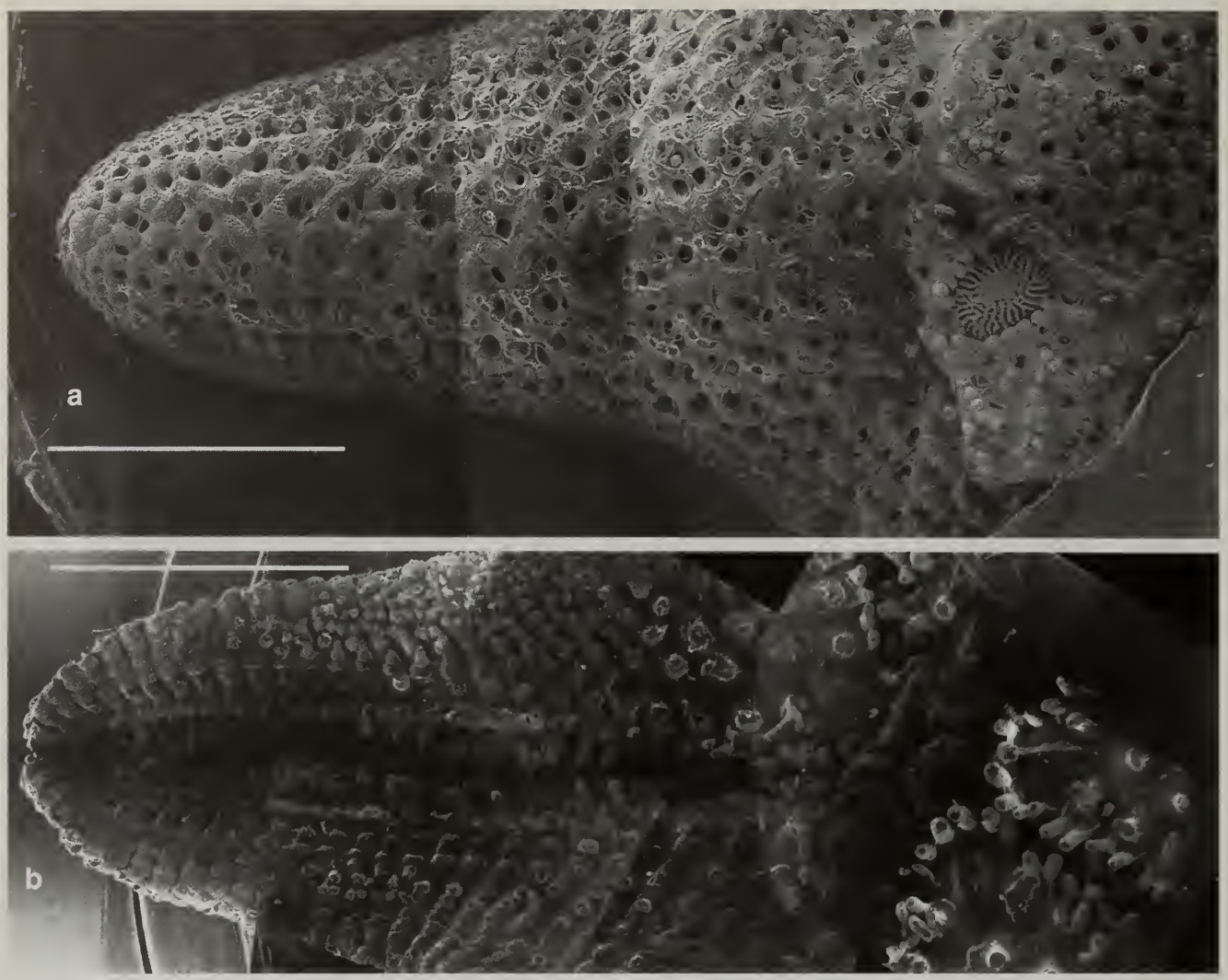

Fig. 4 a, Scanning electron micrograph of the abactinial surface of *Patiriella paradoxa* from Wadi Haart, Sadh, Dhofar, Southern Oman. Scale bar: 5mm; b, Scanning electron micrograph of the actinial surface of *Patiriella paradoxa* from Wadi Haart, Sadh, Dhofar, Southern Oman. Scale bar: 5mm.

rufotincta. During the monsoon period, July–September, the middle shore is richly cloaked with the green alga *Ulva* sp. and brown algae develop on the lower shore. These growths are burnt off by December, and then the intertidal remains almost alga free until the next south west monsoon. It is worth noting that perennial beds of the kelp *Ecklonia radiata* have been recorded off Sadh head (Barratt *et al.*, 1986) approximately 5 km. to the south west of this site. *Ecklonia* may actually occur much closer as fragments were found washed up on the beach.

Paratype 2 was collected on 5.12.86 at Raaha 2.5 km. west of Wadi Ayn at 8 m depth on rocks amongst corals. This site faced south south east and comprised a sandy cove bordered to the east by a ridge of metamorphic rock sloping down to sand at 10 m. The rock ridge was well covered with many scleractinian colonies, especially *Acropora* sp. During the south west monsoon period this 'coral garden' became completely overgrown with the brown alga *Sargassopsis zanardini*. At the time of the collection the *S. zanardini* growths had broken up and dispersed. No *Ecklonia radiata* was seen growing in the immediate vicinity.

DISTRIBUTION. Known only from the type localities on the coast of Dhofar, southern Oman.

REMARKS. Based on arrangement and shape of skeletal plates and their armament, *paradoxa* is without doubt congeneric with *Patiriella regularis*, the type species of *Patiriella*. It differs from that species, as with the majority of its congeners in the form of the radial 'field' of abactinal plates, the high number of papulae per papular area and absence of suboral spines. The absence of suboral spines is shared with four species from the southern Australian coast. Of these *P. parvivipara* is a small, precociously viviparous, pentagonal, cushion-shaped star; *P. brevispina* and *gunni* have six, non-projecting rays, and are more or less cushion-shaped and hexagonal in outline. Additionally, these species differ from *P. paradoxa* in the increased frequency of two spines on each of the proximal actinal intermediate plates, and *gunni* possesses two subambulacral spines per adambulacral plate. *P. paradoxa* may appear to be most closely related to *P. calcar*, differing most obviously in having a more delicate abactinal plating and armament and having 5 instead of 7–11 short rays. Clearly the geographical isolation of *paradoxa* from its congeners has resulted in the evolution of a combination of characters which isolates it within the genus.

ZOOGEOGRAPHICAL CONSIDERATIONS.

The genus *Patiriella*, as accepted herein, is distributed predominently in temperate seas. No fewer than 10 of the 15 species included occur in Australian waters (Rowe & Gates, 1995). Six of the species (*brevispina, calcar, gunni, inornata, parvivipara* and *vivipara*) are endemic to Southern Australia. Two species range across the Tasman Sea between southeastern Australia and New Zealand (*regularis*) or Lord Howe Island and Kermadec Islands (*oliveri*). One species (*pseudoexigua*) is essentially tropical, ranging from northeastern Australia north to Japan. The somewhat ubiquitous *P. exigua* ranges from southern Australia, westward across the southern Indian Ocean to St. Helena Island off southwestern South Africa in the southern Atlantic. Of the other species, *dyscrita* is endemic to South Africa; *calcarata* is endemic to Juan Fernandez Islands; *chilensis* occurs between Chile and Peru and, *fimbriata* is distributed from southern Chile to the Falkland-Magellan area and southern Argentina (A.M. Clark, 1993). With the exception of *fimbriata* which has a known depth range from intertidal to c. 300m, species of *Patiriella* are essentially intertidal, occurring at most to about 30m depth (A.M. Clark, 1993).

The occurrence of a species of *Patiriella* isolated on the Dhofar coast of Oman, in the tropical, northwestern Indian Ocean, is difficult to explain; whether as the result of distributive, accidental or vicariant events.

To seek explanation by a distributive means requires knowledge of reproductive strategies within the genus. Unfortunately, we have been unable to determine reproductive strategy in *P. paradoxa* through examination of the gonads, since the three specimens collected to date were preserved and dried. Since gonopores do not occur on the oral surface (see p. 133), and it is clearly not viviparous, then we assume aboral gonopores occur in *P.paradoxa* and the strategy involves either planktotrophic or lecithotrophic larvae. However, life histories of at least seven species of *Patiriella* occurring in Australia, including *P. regularis* which also occurs in New Zealand have been determined (Byrne, 1991; 1992; Byrne and Barker, 1991). Of these, *regularis* exhibits an indirect/planktotrophic developmental pattern with feeding bipinnaria and brachiolaria larvae; *gunni, calcar, pseudoexigua* exhibit a direct/lecithotrophic developmental pattern with planktonic non-feeding brachiolaria larvae; *exigua* exhibits direct/lecithotrophic developmental pattern with a benthic non-feeding brachiolaria larva; *vivipara* and *parvivipara* exhibit a direct/viviparous pattern of development as intra-ovarian brooders, without larvae. The occurrence on the the Dhofar coast of Oman of *Patiriella* originating via larval distribution from either southern Africa or the Australasian region, even though the nearest congeners are *P. dyscrita* (S. Africa) and *P. pseudoexigua* (recorded as *P. exigua* by Koehler, 1910), from the northeastern Indian Ocean, is difficult to envisage. The present-day water currents of the Indian Ocean must have been established for at least the last 15–10my, following separation of the Indian Ocean (see Adams, 1981; van Andel, 1981). The isolation of *P. paradoxa*, on the Dhofar coast suggests a genetic isolation which is not receiving input from other parts of the generic range.

An explanation of the origin of the temperate-water genus *Patiriella* on the tropical Omani coast in association with a secondary agent is, however, not at first sight, unreasonable to propose. For instance, Dartnall (1969a) considered the New Zealand species *P. regularis* had been introduced into Tasmanian waters amongst oyster spat. The distribution of *P. exigua* from southern African to St. Helena Island, in the south Atlantic, has been attributed, by Mortensen (1933) to probable transport on the holdfasts of the kelp *Ecklonia*, which though not established itself on St. Helena was washed ashore there. A.M. Clark (1992, in A.M. Clark and Downey) considered this a reasonable supposition since *exigua* is not recorded from Ascension Island, to the north of St. Helena where the current is from the east. The occurrence of *Ecklonia radiata*, otherwise known only from around the coasts of South Africa, Australia and New Zealand, which has been recruited to the southeastern coast of Arabia via the deep Antartic current from the south (Sheppard, 1992, in Sheppard, Price and Roberts) might have provided a 'raft' for *Patiriella* to reach the Dhofar coast, originating either from South Africa or the *Patiriella*-species-rich southern coast of Australia. However, such 'rafting' or 'accidental' introductions tend only to extend species range, as it has done with *Ecklonia*. To seek a solution here for *Patiriella* requires invocation of the **subsequent** evolution of the species *P. paradoxa* and extinction of its ancestor on the coast of Dhofar. Once again, the genetic and geographic isolation of *P. paradoxa* would not appear to support such an arguement of its origin on the Dhofar coast, even from its geographically nearest congeners (see above).

The lack of fossil history of the family Asterinidae does not preclude ancient history. It may be more productive, therefore to seek a linkage between the distribution of *Patiriella* (particularly considering its very close relationship with *Asterina* s.s., from the Atlantic, and *Patiria*, from the North Pacific) and vicarient events in the Indian Ocean. The oceanographic and geological configurations of the area appears to have been relatively stable for at least the last 15–10 my (Powell *et al.*, 1981; Adams 1981).

Coincident with this time the complete opening of Drake's Passage (25–15 mya) established the circum-Antarctic current and a sharp drop occurred in surface and bottom sea-water temperatures (van Andel, 1981). It can be concurred that the present-day areas of upwelling, including those within the Indian Ocean were also established at that time. This is of interest for two reasons. Firstly, a major area of upwelling is known off the coast of Dhofar (fig. 2). This produces turbulent, nutrient-rich surface waters and almost temperate conditions (minimum recorded water temperature of 15.9°C near Sadh; Savidge, *et al.*, 1986) which prevail in the coastal region of Dhofar for at least 4 months of the year (June–mid September) (see Currie *et al.*, 1973; Campbell and Morrison, 1988; Miller and Morris, 1988 for details) and this is coincident with the known distribution of *P. paradoxa*. Secondly, the general temperate-water distribution of species of *Patiriella* (as included herein), *Asterina* s.s. (including only species *gibbosa, phylactica, stellifera* and possibly *pancera*; according to FWER, unpublished) and *Patiria* (including species *miniata, pectinifera* and possibly *minor*; according to FWER, unpublished), which appear (with the exceptions of *Patiriella pseudoexigua* and *Asterina stellifera* along the tropical west coast of Africa, part of its range) not to extend into locations much, if at all, above the 20°C isotherm (distribution data taken from A.M. Clark, 1993). The implication of the present-day distribution pattern of these three genera is that their ancestor was more widespread in cooler parts of the Tethyan system (possibly during the later part of the Oligocene epoch (c. 40–25 mya) (see van Andel, 1981)) and before its closure, following which event the structural differences recognised in separating the three genera would appear to have evolved in the fairly discrete geographical isolation which occurred between them. Although the distribution of its congener *pseudoexigua* across the tropics from northeastern Australia to southern Japan is somewhat confounding, the isolated, endemic occurrence of *P. paradoxa* on the southern Arabian coast might be explained in terms of its being a relic. This is all the more likely due to the influence of local seasonal upwelling, providing more temperate conditions, suitable for the genus, at least for part of the year, the

species clearly having evolved to survive year-round conditions on the coast in this tropical part of the world. Upwelling along the west coast of Africa may well account for the extension of *Asterina stellifera* into more tropical regions in the western Atlantic part of its distribution. It will be of interest now to investigate whether other shallow temperate-water echinoderms (other than the globally ubiquitous ophiuroid, *Amphipholis squamata*) (see Price, 1982) or other invertebrate taxa (see Barratt et al, 1984) might be found to occur in the Dhofar region, which might support this thesis, particularly since no other temperate-water distributed taxa appear to have been recorded from the area.

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